THE DUAL PHASE EVOLUTION FRAMEWORK FOR UNDERSTANDING EVOLUTIONARY DYNAMICS IN COMPLEX ADAPTIVE SYSTEMS

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Abstract: Evidence from several fields suggests that dual phase evolution (DPE) may account for distinctive features associated with complex adaptive systems. Here, we review empirical and theoretical evidence for DPE in natural systems and examine the relationship of DPE to self-organized criticality and adaptive cycles. A general model for DPE in networks is outlined, with preliminary data illustrating the emergence of phase changes.

1 INTRODUCTION

Complex adaptive and evolutionary systems exhibit a number of interesting properties such as far-from-equilibrium dynamics, perpetual novelty and sustained diversity. While many advances have been made in understanding specific complex adaptive systems (CAS), a unifying theory of their underlying mechanisms remains elusive. Several conceptual frameworks have been proposed to describe the properties of CAS. These include the concepts of self-organised criticality (SOC) (Bak, 1999; Bak et al., 1988) and the adaptive cycle (Gunderson and Holling, 2002). While these frameworks effectively capture some of the observable dynamics seen in CAS, other properties remain neglected and the causal processes have not been clearly defined.

Previous research has shown that CAS can be described in terms of networks of interacting components (Green, 1993) and that structural properties of these underlying networks may be used to explain many of the processes observed in CAS. Based on this realisation, the notion of Dual Phase Evolution (DPE) was proposed (Green et al., 2006; Green et al., 2000). In short, DPE explains CAS properties such as perpetual novelty and diversity, modularity, and complexity on all scales in terms of recurring phase transitions in connectivity and interaction patterns of underlying networks. DPE processes can be observed across a wide range of CAS of various orders of magnitude: from species

evolution and ecosystem development, to socio-economic systems, to artificial adaptive and optimisation systems.

In this paper we review some of the empirical evidence for DPE and contrast it with other frameworks for understanding CAS dynamics, in particular SOC and the adaptive cycle. We highlight the key differences between these frameworks and DPE and discuss how some processes may be explained in terms of these different frameworks. This presents a step towards providing a holistic understanding of CAS dynamics based on the underlying network properties. To support our arguments we outline a simulation model of energy flow through a network of interacting components. A number of real world CAS can be mapped to this network model. While a thorough analysis of the model dynamics is on-going, the results indicate that DPE processes emerge in the model under a wide range of parameters.

2 DUAL PHASE EVOLUTION

2.1 Examples

Evidence from several fields suggests that phase changes in landscape connectivity form a powerful agent of evolutionary change and innovation. Disasters often mediate long-term changes in the composition of ecological communities, with

established species forming an impenetrable barrier to invasion by novel species until massive population destruction clears the landscape. Palynological data show that changes in species composition in North American forests are consistently associated with major wildfires (Green, 1982). At larger geological timescales, many recent adaptive radiation events are associated with transitions between glacial and interglacial periods that lead to drastic changes in habitat connectivity for a wide variety of species (Willis et al., 2004). Climate-change mediated variations in sea level can cause populations living at specific depths to become fragmented or connected, while temperature and rainfall variation alters the connectivity of lakes and waterways and their ecological communities (Roshier et al., 2001). For example, diverse new species of cichlids emerged in African rift lakes after the last Ice Age isolated local fish populations. Genetic suture zones (areas where locally differentiated populations meet) in many European and North American species including trees, insects, birds and mammals can be traced to population expansion from refugia that were isolated during glacial periods (Swenson and Howard, 2005; Hewitt, 2004). Repeatedly-isolated refugia are associated with speciation events; for example, a meta-analysis of mitochondrial DNA studies in 63 bird species, showed that many adaptive radiations initiated in the Pliocene were completed when glaciers fragmented populations in the Pleistocene (Avise and Walker, 1998). On the mountainous island of Sulawesi, adjacent-living similar species of grasshoppers, macaques, pond-skaters, cicadas, bees, butterflies and beetles are thought to have arisen during periods of habitat fragmentation caused by climate change (Butlin et al., 1998).

At even larger scales, state transitions may be seen in evolutionary dynamics after environmental change. Eldredge and Gould (1972) documented evidence for punctuated equilibria in the fossil record, arguing that biological history is dominated by long periods of stasis with occasional bursts of innovation after mass extinction. These bursts of innovation, according to Gould (2002), are triggered by the removal of ecological specialists, opening up niches for exploitation by the widespread generalists which preferentially survive mass extinction. These generalists then undergo adaptive radiation. In this sense, evolution alternates between long, slow periods of general stability dominated by species selection (stability phase) and brief periods of rapid microevolution where novel adaptations arise (variation phase). There are several possible

explanations for punctuated equilibrium (Gould and Eldredge, 2000). However, the strong geological association between disasters (such as asteroid strikes, vulcanism and climate change), mass extinction and subsequent radiation events suggest that these external drivers are crucial in that they force the switch from stability to variation phases by altering the connectivity of food webs and landscapes.

Simulation experiments confirm this argument. For instance, Paperin et al. present a model (2007) in which organisms normally exist within a connected landscape in which selection maintains them in a stable state. Intermittent disturbances (such as fires, commentary impacts) flip the system into a disconnected phase, in which populations become fragmented, freeing up areas of empty space in which selection pressure lessens and genetic variation predominates. The simulation results show that DPE-like connectivity phase changes can facilitate the appearance of complex diversity in a landscape ecosystem.

Dual phase processes also occur in non-living natural complex systems. For instance, Perkins (Perkins, 2003) describes in an overview article how various kinds of landscape patterns may have been formed by repeated phase changes in several interacting geomorphic processes. A well studied example of such landscapes – the geometric shapes of stones occurring in many polar and high alpine environments – has been investigated by Kesser and Werner (2003) who demonstrated that such patterns may emerge through freeze-thaw cycles that drive an interaction between two feedback processes. In the first process, ice forms in freezing soil, segregating stones and soil by shifting soil toward soil-rich areas and stones toward stone-rich areas. In the second process, stones are transported along the borders of stone-rich domains, which are squeezed and shaped under the pressure of expanding freezing soil. The authors provide a numerical simulation model (Kessler and Werner, 2003) that can reproduce the patterns found in natural landscapes of this kind (Perkins, 2003).

Connectivity phase changes are also the driving force in many artificial CAS. Phase transitions of interaction networks have been implicitly present in many traditional optimisation algorithms in the form of mediation between local and global search. For instance, in simulated annealing (Kirkpatrick et al., 1983; Cerný, 1985) the temperature schedule is used to arbitrate between local and global search steps. Similar ideas have been employed to improve performance in a variety of optimisation techniques

that are prone to being caught in undesirable local optima when applied to non-smooth search spaces. This includes, for instance, the back propagation learning algorithm for artificial neural networks. (e.g. Ramamoorthy and Shekhar, 1989), the Particle Swarm Optimisation algorithm (e.g. Wang and Li, 2004; Liua et al., 2005), Genetic Programming (e.g. Cordon et al., 2002) and Support Vector Machines (e.g. Lin et al., 2008; Sun and Sun, 2005). In the above algorithms the connectivity of the transportation network along which the search proceeds is changed from well connected (global search, exploration) to poorly connected or disconnected (local search, exploitation).

In these artificial optimisation systems, phase transitions occur only once or a few times in one direction. However, natural DPE processes are typified by repeated connectivity phase transitions in both directions. Arguably, optimisation algorithms supplemented with simulated annealing style techniques may be improved by incorporating repeated connectivity phase transitions in both directions. An instance of this approach is a modification of the Cellular Genetic Algorithm (Alba and Dorronsoro, 2008; Whitley, 1993). Kirley et al. (2002; 1998) modified this algorithm to supplement it with insights from population dynamics and landscape ecology. The evolving population was placed in a 2-dimensional cellular automation grid that is subjected to intermittent "disasters" that eliminate all solutions in one part of the grid. As a result, the population becomes fragmented and the gene flow between the sub-populations is diminished or interrupted. This allows the sub-populations to diverge and slows down convergence. Recombination of diverged sub-populations while re-populating areas freed by disasters often leads to discovery of new and fitter solutions. The Cellular Genetic Algorithm modified in this way outperforms the standard Cellular Genetic Algorithm on a number of hard test problems (Kirley, 2002; Kirley et al., 1998).

It should be noted that in this case, the DPE phase transition occurs repeatedly in both directions. Two important interaction networks can be identified within the cellular grid. Firstly, there is the connectivity network between the populated grid cells. The connectivity of this network plays a role in determining the amount of gene (information) flow between different cells. Thus, connectivity in this network influences whether the population evolves as a whole or as divergent sub-populations. The second network is the connectivity network of free grid cells. These cells can be populated by newcomers without substantial competition. During phases where this network is well connected the algorithm has the opportunity to experiment with candidate solutions that may be less fit than some other part of the grid population, but that have potential to evolve towards a different, possibly better local optimum.

2.2 The DPE Framework

A common thread in all of the above examples is that complex properties of systems are mediated by qualitative changes in the connectivity structure of the underlying networks. The connectivity structure can be classified into two main states or phases: "connected" and "disconnected". The "connected" phase is typified by high edge density and short paths lengths. In this phase interactions can therefore occur between most of the network components. In the "disconnected" phase edge density is low, paths lengths are long, and the network typically consists of several disconnected components. Interactions in the disconnected phase typically occur locally or only within strongly connected components.

Since networks are inherent in the structure and behaviour of all complex systems (Green, 1993), a connectivity avalanche (Erdös and Rényi, 1960) underlies many kinds of critical phase changes (Green, 2000). Therefore all such systems can switch between the two above phases. Systems in the disconnected phase tend to be balanced. They may exhibit strong local variability, but typically little large-scale variation. Global responses to external stimuli are constrained, as perturbations cannot propagate far. Systems in the connected phase, in contrast, exhibit less local variability, but significant variation on all scales in the sense that responses to external stimuli are generally hard to predict. The rich connectivity allows perturbations to propagate far, affecting many system parts (Paperin et al., 2007).

DPE occurs when an evolving system repeatedly switches between these two phases (figure 1). Crucial for understanding many DPE systems is the mechanism responsible for these repeated phase transitions. There is much evidence that CAS generally self-organise towards a stable, balanced state. Stabilising forces include lower order dynamics, such as feedback loops, and higher order dynamics, such as selection (in a general sense) (Lenton and Van Oijen, 2002). Analytical (Watson and Lovelock, 1983; Weber, 2001) and computational (Lenton and Van Oijen, 2002) models show that lower-order local dynamics can stabilise

systems over a large range of external forcing, and that higher order local dynamics (evolutionary dynamics) can greatly increase the stabilising effect. The adaptive forces that underlie global stability of CAS also inhibit novelty and change. In particular, selection acting on system components at various scales, as well as on topology and interactions, may drive a system as a whole to a local optimum state, halting innovation (Holland, 1995). Two mechanisms work against such long-term stasis.

Balance Phase
- Loosely connected components
- Selection and other stabilising forces dominate
- Local variability
- Little global variation

Variation Phase
- Richly connected components
- Little local variability
- Response to stimuli unpredictable
- Global variation

perturbation
- modifies network components
- destroys connectivity patterns
- affects relationships

Stable system
- low connectivity
- local interactions

Unbalanced system
- high connectivity
- global interactions

pressure towards stability
- e.g. selection

Figure 1: The mechanism of Dual Phase Evolution. Systems flip between loosely connected balance and well connected variation phases. Perturbations and external stimuli unbalance stable systems, variation facilitates evolutionary exploration, and internal pressures drive the system into a new stable state.

One mechanism is co-evolution. Local adaptation of system components by selection may affect the selection criteria for other components, which will adapt as a result. This in turn affects the fitness landscapes of the components that initiated the changes. Such feedback loops may form sources of perpetual novelty. However, it is not clear that co-evolution fully accounts for the innovation observed in many natural CAS. For instance, analytical models (Gavrilets, 2004) suggest that selection, not variation, drives speciation. Co-evolutionary feedback loops are likely to rapidly lead to stable system states. Once such a local optimum is reached, selection makes successful variations highly unlikely (Gavrilets, 2004).

A second mechanism that may underlie continual novelty in CAS is disturbance. As discussed in section 2.1, evolutionary innovations often coincide with external perturbations. External disturbances may affect both system components and interaction networks, thus moving systems away from local optima. Densely connected interaction networks,

while providing many stabilising interactions, also facilitate disturbance propagation. The complexity of dense interaction networks makes large-scale responses to disturbances essentially unpredictable.

Once away from a local optimum, systems enter a variation phase. Chance variation of local components may provide better adaptation to local constraints; selection facilitates proliferation of such changes within networks. Selection then amplifies variations and eliminates destabilising interactions, reducing connectivity, and components and their interactions self-organise towards new local optima.

Over time, surviving system components develop new interactions, increasing the connectivity of interaction networks that survived previous disturbances. Eventually, the system enters a new balance phase.

While some parts of a system may be completely or partly reorganised during a variation phase following a particular disturbance, others remain stable. These stable parts may form new interactions and assume new roles, acting as functional components during a variation phase. A simulation by Paperin et al. (Paperin et al., 2008) demonstrated that DPE can result in modular networks. We conjecture that this mechanism may also contribute to emergence of hierarchical organisation in CAS.

2.3 DPE and Self-organised Criticality

DPE can be linked to several other key concepts in CAS theory. One such concept is Self-Organised Criticality (SOC) (Bak, 1999; Bak et al., 1988). Under SOC, CAS self-organise to a critical state where system behaviour emerges from propagation of stimuli via local component interactions. SOC suggests that CAS evolve towards the "edge-of-chaos" (Langton 1990; Langton 1991), a transition state between the stasis of equilibrium systems and the unpredictability of chaotic systems.

Sizes of stimuli propagation avalanches in SOC systems follow a power distribution, leading some researchers to argue that power-distributed data imply SOC. Models (Bak, 1999) suggest ways in which certain natural systems may exhibit SOC dynamics. However, the general applicability of SOC remains doubtful. Other processes also lead to power-law distributed data. For example, it has been proposed (Bak and Sneppen, 1993) that the biosphere self-organises to a critical state, potentially explaining punctuated equilibria (Eldredge and Gould, 1972). However, (Newman, 1997) demonstrates a non-critical extinction model that yields a power-law with an exponent closer

(Lenton and Van Oijen, 2002) to the empirical punctuated equilibria data. SOC also appears to require fine-tuning of an order parameter (de Carvalho and Prado, 2000; Sornette et al., 1995), and the applicability of SOC to non-conservative systems (de Carvalho and Prado, 2000; Kinouchi and Prado, 1999) remains unclear.

To describe DPE using the SOC-vocabulary: CAS develop to a balance-state, where they are stabilised by internal forces (e.g. selection, negative feedback mechanisms). External disturbances repeatedly push a system *across the critical region*, to a chaotic state (in the sense that systems responses to stimuli are unpredictable), from which the system returns to a new balance-state, accumulating order and complexity on the way (figure 2).
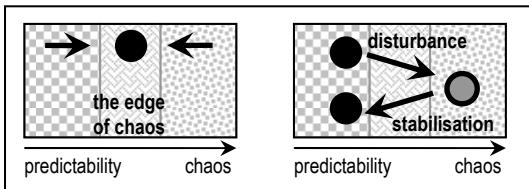
Figure 2: Dual Phase Evolution vs. Self-Organised Criticality. SOC-theory suggests that CAS self-organise to a transition state between the general stasis of equilibrium systems and the random behaviour of chaotic systems (left). According to DPE, CAS are repeatedly pushed from a balance-phase to a variation-phase by external disturbances (right). The X-axis on this metaphoric illustration represents the degree of predictability of system's responses to stimuli.

Often, SOC is used to express that a system has self-organised to a specific state, without describing the underlying processes. The DPE framework attempts to define the internal forces responsible for system states. In this sense some systems may self-organise to a critical state through DPE. For instance, scale-free networks (Albert and Barabási, 2000) are traditionally associated with SOC because their node degrees follow a power distribution. Traditionally, scale-free topologies were thought to arise through preferential node attachment during network growth (Albert and Barabási, 2000). However, scale-free topologies can arise through DPE in networks of constant size (Paperin et al., 2008). Networks developed this way may underlie some systems with apparent SOC dynamics.

2.4 DPE and the Adaptive Cycle

An influential concept in CAS theory is the adaptive cycle (AC) (see Gunderson and Holling (2002)). The AC extends the idea of ecological succession

(Gleason, 1927), and is predominantly applied to ecological and socio-ecological systems, especially with reference to ecosystem management and resilience. The AC identifies 4 phases in ecological succession:

- a growth and exploitation phase (designated r), in which new or freed-up areas and niches are rapidly populated by opportunistic organisms;
- a conservation phase (K) signified by competition, selection and resource accumulation;
- a collapse or release phase (Ω), in which accumulated resources are catastrophically released, often mediated by disturbances;
- a reorganisation phase (α) in which the remains of an Ω-collapse are reorganised and restructured.

The AC concept attributes typical CAS properties to each phase. Resilience against external forcing is expected to be high during r and α phases but low during K, while resource availability is high during α and K phases, but low during r and Ω. Connectedness of control variables is maximal near the end of a K-phase. The AC provides a descriptive formalism for self-organisation in ecosystems. DPE theory distils concepts of the AC that are applicable to a wider range of CAS and provides a causal model based in network theory.

The balance phase in DPE loosely corresponds to the r-K transition in AC. This phase is signified by stabilising selection, increasing connectivity, and growing potential for disturbance propagation. The variation phase in DPE loosely corresponds to the Ω-α-r transition in AC. This is a phase of innovation and re-organisation of underlying networks.

Notably, connectedness in AC refers to the richness of interactions of control variables. In fact, there may be several interaction networks with different connectivity regimes within a system at any one time. For example, species in food webs and populations in landscapes form interaction networks that act simultaneously on the same groups but may have very different topologies. The structural properties of the interaction network of control variables may thus be different from the interaction network of components where disturbances propagate; a comprehensive CAS theory must account for this fact.

3 A DPE SIMULATION MODEL

To further investigate the DPE process and the role of disturbances and connectivity in CAS we created

an abstract model of resource flow through a network. We briefly discuss the model and some preliminary results here. The main objective of this paper is to review the empirical evidence for DPE and to discuss its relationship to other CAS theories. The space limit does not permit us to examine the model in greater detail and more detailed results will be published elsewhere (paper in preparation).

The model consists of a number of nodes connected via directed edges. Energy flows along edges and nodes require energy to sustain themselves. All nodes in the system are designated "component nodes", except for one, designated the "source". The source node does not require energy, instead it produces a constant amount of energy at each iteration. Energy flows along downstream connections attached to a node. Each model iteration consists of three stages: energy propagation, node maintenance and structural modification.

Energy Propagation. At the start of each iteration each component node c passes a proportion of its stored energy f_c along its downstream connections. Total energy propagated downstream by c is $d_c = f_c \times (1 - r_c)$, where the retention factor $0 \leq r_c < 0$ is a random number drawn when c is created. The remaining energy $(f_c - d_c)$ is retained by the node. If c has no outgoing links, all of f_c is retained. Nodes at the end of downstream edges of c compete for the energy propagated by c. Competition for resources in real systems requires energy. This is modelled by a competition cost factor $k_c = 1 / (1 + e^{2 \times (l_c - i_c)})$, where l_c is the number of downstream edges from c, and $i_c > 0$ is a random number drawn when c is created, it is the maximum value of l_c such that most energy is not wasted by competition expenses. Each of the l_c downstream edges receives an equal amount of $(d_c \times k_c / l_c)$ units of energy from c. Any energy conversion in nature comes with a loss. To model this, every edge g has a flow efficiency value w_g associated with it, such that the amount of energy actually arriving at node c_q from node c_p is $u_{q,p} = (d_c \times k_c / l_c) - w_{g(p,q)}$, where $g(p, q)$ is the edge from c_p to c_q and $w_{g(p,q)}$ is a random number drawn when g is created.

Node Maintenance. After all nodes have propagated energy downstream, the total available energy f_c at each component node c is equal to the amount of energy retained by c during the propagation stage plus the sum of the incoming energy from all upstream edges. Every c has an associated maintenance cost $m_c > 0$ selected

randomly when c is created. To maintain its existence, every c expends m_c energy units per iteration. If $m_c > f_c$, then c dies and is removed from the system along with all connected up- and down-stream edges. The source node never dies. If c accumulates a large amount of energy, it reproduces. This happens by creating a duplicate copy h of c. The offspring h receives the same number of edges as c. Each of these edges may be connected either to the respective partner of c, or to any other random node with equal probability, thus modelling random mutation. The reproduction process consumes an amount of energy significantly larger than m_c and remaining energy is divided evenly between c and h.

Structural Modification. Every iteration, a new component or a new edge is introduced into the network with a small probability. When a new component c_n is introduced, for every existing node p, an edge $g(p, n)$ is added with a small probability. New edges connect two randomly selected existing nodes. Similarly, nodes and edges are removed from the network with a small probability at each iteration simulating external disturbances.

The presented model captures major features of resource flow dynamics in several real-world CAS. For instance, the energy flow through food webs in ecosystems follows patterns very similar to those described here. Resource flow between primary and intermediate producers, and end-consumers in economies follows a similar pattern. Thus, the results obtained form our abstract model allow conclusions about a variety of CAS.

3.1 Results

Model dynamics explored under a range of parameter values coincide with the behaviour expected under the DPE framework. A detailed discussion is beyond the scope of this paper, but we briefly overview some of the results here. Some indicators of network dynamics are the number C of component nodes, the total amount E of energy stored by all component nodes in the system, and the network edge density D. The maximum node age A is an indicator on internal stability of the system.

In the absence of external disturbances (probability of random node and edge removal is zero), C and E are lower on average compared to cases with disturbances. This initially surprising result can be explained by the DPE process. In the absence of disturbances unfavourable configurations can only be removed through node starvation. In the presence of disasters that propagate through the

system by cutting off nodes and reducing connectivity, the remaining network sub-structures exhibit more efficient and robust connectivity patterns. Additionally, newly created nodes can better compete with established nodes that stored significant amounts of energy when all nodes can equally be affected by disturbances. This increases potential for innovation and for discovery of even more stable configurations.

Another consistently emerging pattern is that low values of D strongly correlate with high values of C and E: a small number of connections is enough to efficiently distribute the energy across the components and additional edges lead to excessive energy expenditure due to unnecessary competition and flow friction along the edges (figure 3).
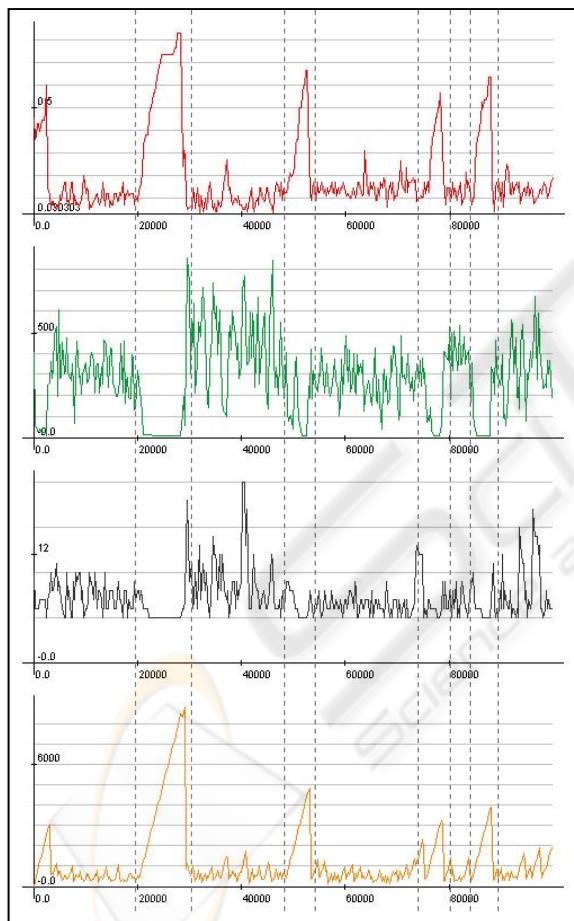
Figure 3: A typical simulation run. Shown are (from top to bottom): edge density D, total stored energy E, number of component nodes C, oldest node age A. Mean node age (not shown) strongly correlates with A. The x-axes represent iterations. The vertical dashed lines are a visual aid to stress apparent phase changes.

In a typical run A is normally low (< 1000), indicating internal instability. Over time, robust network configurations are discovered, signified by a growing value of A (>> 1000). Edge density in these stable configurations grows, making them less efficient and more susceptible to catastrophic change caused by structural modifications. Eventually, E reaches a very low value and the stable configurations collapse leading to the next variation phase (figure 3). This behaviour is in line with the predictions of DPE. However, in most of our experiments the variation phase was significantly longer than the DPE framework predicts. This observation may be explained by the absence of higher order stabilising control mechanisms such as selection between network configurations. Further experiments will test this conjecture.

4 CONCLUSIONS

Previous work shows that complex adaptive and evolutionary systems can be represented as networks of interacting components and that many interesting properties of CAS may be explained in terms of a network theoretical framework termed Dual Phase Evolution. According to DPE, networks underlying complex systems adapt and self-organise by alternately switching between two phases: a phase of high connectivity dominated by global component interactions and a phase of low connectivity dominated by local interactions.

Here we demonstrated that DPE may provide a causal explanation for known CAS properties typically expressed through other established descriptive formalisms. Simulation results indicate that DPE-like phase changes arise in an abstract model of resource flow in a network that is representative of a variety of systems. This work provides a step towards an integral understanding of CAS and suggests that more advances can be made by further empirical and theoretical studies of Dual Phase Evolution.

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